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Hominid Palaeobiology: Have Studies of Comparative Development Come of Age?

BERNARD WOOD
Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, The University of Liverpool, Liverpool L69 3BX, England, United Kingdom

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ABSTRACT It is 70 years since Adolf Schultz urged his colleagues to consider how studies of primate growth and development could help them interpret the course of human evolution. This paper considers the evolutionary context of comparative growth studies. It compares and contrasts aspects of the ontogeny of living modern humans and chimpanzees, and considers whether relatively simple models of heterochronic change can account for the modifications which have taken place during the course of human evolutionary history. © 1996 Wiley-Liss, Inc.

> With these few and scattered observations on the relation of the growth of primates to man's evolution . . . it is hoped to have at least stimulated further investigations and thought—perhaps criticism—in this promising field. (Schultz, 1924, p. 163)

Thus wrote Adolph Schultz, just over 70 years ago, at the conclusion of a paper entitled "Growth studies on primates bearing on man's evolution."

The study of human evolution is a threefold process. It involves tracing the events which occurred during hominid phylogeny, the pursuit of information about the context of those events, and the investigation of the processes which helped to shape them. This paper examines the extent to which those who came after Schultz have taken up his challenge to relate the *process* of development to the *events* of human evolutionary history. In what ways can development contribute to the study of human evolutionary history? What contribution have studies of comparative development made to our understanding of that history in the seven decades since Schultz's pioneering essay? Has the "promise," which Schultz referred to, been realised?

BACKGROUND

Development, or ontogeny, is the process of moving, in one and the same individual, from a morphologically undifferentiated group of cells to an organism which is usually larger, morphologically more heterogenous, and more complicated in its organisation. The process of development is itself a complex one, but it can be reduced to three main elements: *differentiation,* which is the emergence of generally irreversible, inherited, differences between somatic cells; *relative movement,* which includes the migration of cells, tissues and even organs; and *growth,* which is an increase in mass and size.

The most obvious link between development and evolution is the self-evident one, namely, that evolution occurs through modifications which have been made to the programme of ontogeny (Raff and Wray, 1989), which result in a change in the phenotype. These modifications take many forms, but

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they can be simply reduced to two categories. In the first, a change in the phenotype occurs because of alterations to the genes which determine specific structural details of the phenotype. An example of such a morphological innovation would be the introduction of novel structures typical of vertebrates which apparently result from the duplication of genes in the "primitive" homeobox cluster (Garcia-Fernandez and Holland, 1994). The second category of modification is when alterations are made to the timing of the events which occur during ontogeny. The changes in this second category are usually referred to as examples of *heterochrony.* Heterochronic changes can be further subdivided into phenotypically "global" acceleration, or deceleration, of development relative to the time when growth ceases, and the advancement, or retardation, of the development of morphological characters, relative to one another. Gould (1977) and Shea (1988) provide useful summaries of the subcategories of heterochronic change. Most of heterochronic change can only be expressed in relative terms, but because the development of some tissues can be related to astronomical time (Dean et al., 1993a), it is possible to trace changes in the absolute chronology of some developmental events through evolutionary history (see below).

This review is intended to set the stage for the more focused contributions which comprise the following symposium on hominoid ontogeny, organised by Linda Winkler and Bob Anemone. It will discuss, perforce very briefly and selectively, whether comparative studies of primate development have helped to improve our understanding of both the evidence of, and the evidence for, human evolution. Have, for example, comparative studies thrown any light on the proximate mechanisms involved in the changes which occurred during the course of human evolution? What part have such studies played in attempts to reconstruct the life history of early hominid species?

COMPARATIVE EVIDENCE

If, for the sake of argument, we accept the burden of much of the recent evidence about DNA sequence analysis, which suggests that modern humans and the chimpanzees are more closely related to each other than to any other living ape (Goodman et al., 1994; Ruvolo, 1994), then the phenotypic differences between modern humans and the living chimpanzees must stem from evolution which has occurred in the two lineages subsequent to their divergence from their hypothetical common ancestor. While it is true that, as yet, we have no fossil evidence for a creature that is likely to be the common ancestor of *Homo* and *Pan,* evidence from fossil remains which sample a species of what is probably a new genus (White et al., 1995) from the very earliest stages of human evolution (White et al., 1994) suggests that such a common ancestor is likely to have been more like living *Pan* than living *Homo.* Thus, it is appropriate to explore the differences between the development of *Homo* and *Pan,* for these differences, or variants of them, may provide clues to the processes which helped to fashion the phenotypes of extinct early hominid taxa and the more recent species which are generally included within the genus *Homo.*

The aspect of primate comparative development which is most relevant to human evolutionary history is information about the dentition. There are three reasons for this. First, the durability of dental remains mean that they are more likely than developing bones to survive into the fossil record. Second, the developmental history of teeth is retained in the adult; such is not the case with the majority of the bony skeleton. Third, because this retained dental developmental history can be linked with astronomical time (see Beynon and Dean, 1988, for a review), researchers are able to calibrate events in tooth growth and development (Dean et al., 1993b; Dean and Wood, 1981; Smith, 1994a). This potential, and the evidence for close evolutionary links between *Homo* and *Pan,* makes it particularly important to secure good data about the dental developmental history of chimpanzees of known chronological age. The recent accumulation of such data sets (Anemone et al., 1991; Conroy and Mahoney, 1991) constitutes an important advance in our understanding of the comparative context of early hominid and modern human development.

The differences in the rate and pattern of dental development between *Homo* and *Pan* have been recently reviewed by Smith (1992) and Macho and Wood (in press). Although both *Homo* and *Pan* are in Smith's "live slow, die old" category, it is evident that no living primate matches extant *Homo* in the degree of its global growth retardation. Schultz had made this clear in his well-known diagram comparing the absolute durations of four subdivisions of the lifespan of five categories of living primates (Schultz, 1960). He predicted that "early man" would "live faster and die younger" than modern humans. Smith has shown that this is indeed the case for taxa attributed to *Australopithecus*. In addition, she has also developed Schultz's general approach by examining whether the pattern, or sequence, of development is correlated with the rate of growth. Her conclusion is that for some aspects of development it is, and in others it is not. Apparently there is variation even within a single system like the dentition. For example, Smith demonstrates that the "replacement" teeth, the incisors, canines, and premolars, erupt relatively early in those primates with a slow growth rate. These changes in relative rate result in there being less overlap between the deciduous and permanent molar teeth, and thus there are consequent differences in the overall sequence of tooth development (Smith, 1994b). Schultz had also commented on this phenomenon, and had attributed the differences in eruption sequence of *Homo sapiens* and *Pan* to the poor durability of the deciduous teeth and the consequent need for long-lived primates to replace their milk teeth relatively early before they were rendered ineffective by excessive wear (Schultz, 1960). Smith pays tribute to Schultz's perspicacity by suggesting that "Schultz's explanation continues to hold up today, even under the weight of new data" (Smith 1992, p. 140; but see Simpson et al., 1990, for an alternative view).

FOSSIL EVIDENCE

Much of the important evidence for hominid evolution has been discovered since Schultz's pioneering paper in 1924. It is a coincidence, but surely a propitious one, that it was also in 1924 that Raymond Dart recognised the significance of the child's skull which had been recovered from the limeworks at Taung, in what was then Bechuanaland (Dart, 1925). This specimen has subsequently become one of the main foci of debate about what can, and cannot, be inferred about the ontogeny of fossil hominids. This is ironic, because discussions about the significance of the Taung skull have often been prefaced by the admission that its immaturity was an impediment to those who were concerned with unravelling its relationships with other early hominid taxa. The realisation that juvenile material offered hitherto unobtainable access to information about the life history of early hominids was a long time in coming (Smith, 1989, and see below; but see Smith et al., 1995). Likewise, the appreciation that immature early hominid specimens could provide a series of "snapshots" of the evolution of the apparently unique (at least within the primates) ontogeny of modern humans, has only latterly been realised (Bromage and Dean, 1985; Smith, 1986, 1994b; Beynon and Dean, 1988; Conroy and Vannier, 1991).

The difficulty that all studies of early hominid development have to grapple with is that the only sensible comparators are the developmental sequences of the dentition of modern humans and the extant ape species. Thus, the distinctive developmental sequences of the early hominids have to be expressed in terms of how well they conform to "human" and "ape" standards. Some workers are sceptical of claims that the sequence and timing of "human" and "ape" dental development are sufficiently distinct to justify such comparisons (Mann et al., 1987, 1990; Simpson et al., 1990; Lampl et al., 1993). The challenges of the sceptics have duly stimulated responses. The work of Simpson and his colleagues has been responded to by Anemone and Watts (1992), and the conclusions of Mann and Lampl have provoked a robust response from Smith (1994b). The responses, and other studies besides (Kuykendall et al., 1992), have concluded that there are significant differences between the dental development of *Homo* and *Pan*. These are reviewed in Macho and Wood (in press). However, the general point made by Mann

and his colleagues, that intraspecific variation in dental development needs to be taken into account when establishing the parameters of the dental ontogeny of comparative taxa, is well taken. Yet, despite that caveat, there are no grounds for abandoning attempts to investigate and analyse the patterns of early hominid dental development. There are differences between modern human and great ape dental development, and it is only through examining the fossil record that we have any realistic chance of discovering how and when the differences between *Pan* and *Homo* became established.

Other aspects of comparative cranial development have also contributed to our understanding of the hominid fossil record. Two examples come to mind. The first is a study of cranial growth which has enabled researchers to predict the adjustments that would have been required to bring about the changes in the facial phenotype observed in the fossil record (Bromage, 1989, 1992). The second is a cross-sectional study of the changes in the cranial base which occur during ontogeny in modern *Homo, Pan, Gorilla,* and *Pongo* (Dean and Wood, 1984). The latter investigation concluded that some aspects of the growth patterns in *Homo, Pan,* and *Gorilla* are sufficiently similar to allow us to predict the changes that were likely to have occurred during the ontogeny of extinct hominid taxa. If these assumptions are applied to the cranial base of an immature hominid like Taung, it is thus possible to extrapolate to the adult morphology. In the case of Taung, the "extrapolated" morphology is consistent with that observed in adult specimens of *Australopithecus africanus* (Dean and Wood, 1982). The predicted adult form of the cranial base of *A. africanus* does not resemble the cranial base of the adult *Paranthropus robustus.*

PROCESS

Aristotle was apparently the first investigator (Gould, 1977) to link ontogeny with phylogeny, but the connections he traced were not investigated further until the nineteenth century (Meckel, 1811; Serres, 1824; von Baer, 1828). Haeckel considered the connections between phylogeny and ontogeny to be "of a profound, intrinsic and causal nature" (1874, p. 6) and stressed the importance of one aspect of heterochrony, acceleration, in his "biogenetic law" (Haeckel, 1866). When Bolk (1926a) reviewed the link between development and phylogeny in the context of human evolution, he stressed the importance of the retention in modern humans of the juvenile features of our ancestors, and invoked the mechanism of retardation to explain the genesis of an impressive list of adult human characters (Bolk, 1926b).

Since Schultz's contribution some 70 years ago, Gould (1977) has summarised the history of ideas about heterochrony, and has gone on to make his own suggestions about how heterochronic processes may have been involved in the course of human evolutionary history. Gould's analysis has been widely cited, but apparently has not always been correctly interpreted (Godfrey and Sutherland, 1995). Gould suggested that neoteny, and specifically retardation, was the pervasive mechanism which operated on an ancestral ape-like developmental history, and that such heterochronic changes resulted in the emergence of the characteristics of the modern human phenotype. This hypothesis was tested in the context of the cranial base by studying the temporal changes which occurred in series of immature crania belonging to *Homo, Pan, Gorilla,* and *Pongo* (Dean and Wood, 1984). Because the pattern of development of this region is similar in several non-human taxa closely related to modern humans (see above), the authors argued that it is reasonable to infer that the same pattern characterised the ancestral hominid condition. On the basis of their observations, Dean and Wood concluded that the form of the modern human cranial base could not have been derived by general retardation. The cranial base of adult modern humans is thus not explicable as a generalised paedomorphic phenomenon operating on an initial morphology like that of infant modern great apes.

Once the distinctive features of the dental morphology of the major fossil hominid taxa had been established, it was appropriate to examine whether they could have arisen as the result of a relatively simple change in the regulation of dental development. For

example, it became apparent that the best developmental analogy for the large-crowned, rapidly growing postcanine teeth of the "robust" species, *Paranthropus boisei,* is the pattern of rapid enamel formation that is observed in the deciduous molars of modern humans (Beynon and Wood, 1987). Those authors suggested that a relatively simple change in regulation, which resulted in the permanent teeth of *P. boisei* growing like their deciduous counterparts, might be the developmental basis of the postcanine megadontia which is especially apparent in that taxon (Wood and Abbott, 1981; McHenry, 1984).

There is clearly considerable scope for the further study of the development of enamel in early hominids (e.g., Ramirez-Rossi, 1993; Macho and Wood, in press) as well as of the other dental tissues that preserve their growth history into adult life. Indeed, so rapid are the advances in molecular developmental biology (Weiss, 1993), that it may, before too long, be possible to specify the detailed changes in genetic regulation which are likely to have been the proximate mechanisms for evolutionary change (Wood, 1995).

LIFE HISTORY

No matter how good the fossil record, most researchers were reconciled to the fact that some of the most interesting aspects of the biology of extinct hominid taxa, including the ability to reconstruct maturation in anything other than relative terms, would always be "unknowable." However, the ability to relate enamel development to astronomical time, by counting the numbers of cross-striations and Striae of Retzius, together with the discovery that the time of eruption of some teeth is correlated with the timing of other events in development (Smith, 1989, 1991), have now provided a potentially powerful tool for comparing the rate and pattern of development of extinct hominid taxa. For example, it is now possible to predict, with reasonable accuracy, the length of gestation and the ages of onset of weaning and the attainment of sexual maturity (ibid.). It has also been shown that brain volume and mass are correlated with the age of eruption of the first molar (Smith, 1989). This empirical association has important implications for those who study the nature of the modifications to development which have occurred during human evolution. However, when the bases of the prediction equations are examined in more detail, and when the confidence intervals are calculated, it is evident that the link between brain mass and dental development is not strong enough to be able to use brain mass to unequivocally classify hominid dental development as "human" or "apelike" (Smith et al., 1995). Nonetheless, even a weak link may be of practical help for palaeoanthropologists. For example, it can be used by taxonomists to judge the likelihood that jaws from which the age of first molar eruption can be estimated, can be associated with cranial vaults, from which brain volume can be determined.

The potential provided by the study of the developmental indicators of early hominids is particularly evident when such methods are applied to well-preserved specimens which retain evidence from more than one "system." The detailed study of the relative development of the immature KNM-WT 15000, the juvenile male attributed to *Homo erectus* (or *Homo ergaster*) from West Turkana (Smith, 1993), is a case in point.

CONCLUSIONS

Much progress has been made since Schultz "used ontogenetic conditions in an attempt to elucidate certain questions of human evolution" (Schultz, 1924, p. 149). But what questions, if any, have been resolved by workers in the intervening 70 years?

The only systems for which we are close to understanding the proximate mechanisms of growth and development, the modification of which is the basis of evolutionary change, are those involved in the formation of the teeth (Macho and Wood, in press) and the cellular activity which controls the growth in size, and the ontogenic change in shape, of the face (Bromage, 1989, 1992). For the teeth, we now know that there are a finite number of mechanisms that can be adjusted in order to modify the volume of enamel secreted and thus determine the size of the crown. Relatively and absolutely enlarged postcanine tooth crowns are one of

the diagnostic features of *Australopithecus, Paranthropus,* and primitive *Homo* taxa, but at present we do not know whether this megadontia is developmentally homologous in the three genera. If the species in all three genera achieve their megadontia using similar developmental mechanisms, then that is strong, but not conclusive, evidence that all the taxa belong to the same clade. Conversely, if, for example, the megadontia seen in both the regional species representatives of *Paranthropus* has a different developmental basis, then inclusion in the same clade and genus would be difficult to defend.

When evidence about dental development is pooled with comparative data about cranial bone growth and development, it is difficult to sustain the hypothesis that the peculiar features of the human cranium resulted from a single, relatively simple modification to "global" heterochrony. For example, enamel deposition has been shown to exhibit different characteristics in different parts of the same tooth, to say nothing of the same tooth type. It is apparent that no single heterochronic change can be invoked to convert *Pan*-like dental development into a modern *Homo*-like one (Macho and Wood, in press).

There is no shortage of questions to challenge future researchers. What part does body mass play in the apparent linkage between brain size and the age of tooth eruption? Are growth patterns taxonomically valent characters? Do teeth measure astronomical time as well as some researchers claim they do? What should we infer from the apparent conjunction of relatively small brain and a mostly modern human-like pattern of development that are apparently combined in early African *H. erectus*? Did a modern human rate and pattern of development precede an anatomically modern human morphology? Answers to questions such as these will come when observations made on fossils are set in an appropriately comprehensive and detailed comparative framework. There is nearly always a tendency to rush to interpret the fossil record before such a comparative framework has been assembled, but such an approach rarely results in a deeper understanding of evolutionary history. We must redouble our efforts to ensure that we understand the living before we try and interpret the dead.

Schultz's 1924 paper is seldom cited by contemporary authors, but, as in so many other aspects of primatology, it is clear that 70 years ago his extraordinary vision had enabled that great primatologist to appreciate the enormous potential of comparative studies of growth and development. The final paragraph of the 1924 article contains propositions that are not out of place today. I feel confident that Adolf Schultz would have been excited to realise that, 70 years on, studies of comparative development continue to reveal their potential for interpreting the course of human evolutionary history.

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